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Karyotypes and Systematics of the Lizards in the *variabilis*, *jalapae*, and *scalaris* Species Groups of the Genus *Sceloporus*

CHARLES J. COLE[1]

ABSTRACT

Karyotypes of 11 species of *Sceloporus* are described and illustrated. Lizards included are all species of the *variabilis* group as recognized by Smith (1939), all species of the *jalapae* and *scalaris* groups as recognized by Thomas and Dixon (1976), and *Sceloporus siniferus* of the *siniferus* group (for comparisons). The lizards examined include four of the seven species placed in the genus *Lysoptychus* by Larsen and Tanner (1975), karyotypes of the other three species of which I described earlier.

Data from karyotypes and other morphological characteristics suggest the following: (1) *Lysoptychus* is a junior synonym of *Sceloporus*; (2) the *variabilis* group is distinctive; (3) *S. teapensis* is not specifically distinct from *S. variabilis*; (4) the *variabilis* group includes *S. variabilis*, *S. chrysostictus*, *S. couchii*, *S. cozumelae*, and *S. parvus*; (5) the species in the *jalapae* group (*S. jalapae*, *S. ochoterenae*) are very similar to each other; and (6) the *scalaris* group (*S. scalaris*, *S. aeneus*, *S. goldmani*) is distinctive.

INTRODUCTION

The *variabilis* group is one of 15 species groups that Smith (1939) recognized as comprising the iguanid genus *Sceloporus*. Thomas and Dixon (1976) proposed a sixteenth group, the *jalapae* group, to contain two species that Smith had assigned, with others, to the *scalaris* and *siniferus* species groups. In contrast, Larsen and Tanner (1974, 1975) considered 13 subgroups distributed among three major groups as best reflecting relationships of the species that Smith (1939) and other authors included in *Sceloporus*. Although Larsen and Tanner did not describe and define their groupings in detail, in 1975 they resurrected the genus *Lysoptychus* Cope, 1888 for one of their major groups. Among the seven species they assigned to *Lysoptychus* are two of the five species that Smith (1939) placed in the *variabilis* group and both species that Thomas and Dixon (1976) recognized in the *jalapae* group.

In the course of investigating the karyotypes of *Sceloporus*, I have examined chromosomes from representatives of each of the species in the *variabilis* group (as recognized by Smith, 1939), the *jalapae* group (as recognized by Thomas and Dixon, 1976), and the *scalaris* group (as recognized by Thomas and Dixon, 1976). The karyotypic variation observed is useful in interpreting relationships of these lizards, and the relationships indicated are rele-

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vant to the question of whether the genus *Lysoptychus* should be recognized. Therefore, I present the available data for these three species groups together in the present paper, although I have not yet examined representatives of both sexes for all the species.

Karyotypes of 11 species of *Sceloporus* are illustrated for the first time. Although none of these has been described in detail before, the diploid chromosome number of *Sceloporus scalaris* was listed by Lowe, Wright, and Cole (1966, table 1), and chromosomes of species in the *variabilis* group were discussed by Cole (1971a, p. 4).

ACKNOWLEDGMENTS

This work was made possible by the generosity of numerous friends and colleagues who collected many of the specimens examined, sometimes under trying field conditions, and who extended the extra efforts necessary to get them to me alive and in good health specifically for chromosome studies. I thank Dr. James E. DeWeese, Mr. J. R. Glidewell, Drs. Harry W. Greene, Charles H. Lowe, Clarence J. McCoy, Michael D. Robinson, Messrs. Philip C. Rosen, Wade C. Sherbrooke, Ms. Grace M. Tilger, Ms. Carol R. Townsend, Dr. Robert Wayne Van Devender, Mr. Tim Walker, and Dr. John W. Wright. In particular, I thank Dr. Robert L. Bezy, whose extensive assistance included rebuilding a tin roof, and Mr. Philip V. Colbert, who provided an entire summer of his own time assisting me in the field. Most recently, Mr. Ernest A. Liner and Dr. Ralph W. Axtell sent me a series of *Sceloporus goldmani*, collected by them and Dr. Allan H. Chaney, which completed representation of the *scalaris* group. I am grateful to Ms. Carol R. Townsend for many of the chromosome preparations. On various occasions, Dr. Rodolfo Hernández Corzo and Dr. Antonio Landazuri Ortiz, Departamento de Conservación y Propagación de la Fauna Silvestre, provided permits for collecting in Mexico.

METHODS

This report is based on the examination of chromosomes in more than 350 cells from 69 lizards (39 males, 30 females). For most of the lizards, chromosomes of bone marrow and testicular cells were prepared for study by means of the colchicine, hypotonic citrate, flame-dried procedure used by Patton (1967), slightly modified for lizards (Cole and Leavens, "1971" [1972]). The *S. goldmani* required different handling because all were juveniles. I used intestine and spleen of the male (suggested by John W. Wright, personal commun.) and, for the others, whole blood culture incubated at 30° C. for 72 hours in Chromosome Medium 1A (with phytohemagglutinin) of Grand Island Biological Company (suggested by David Cundall, personal commun.).

Chromosome terminology follows earlier usage for *Sceloporus* (Cole, 1970). When I state that the karyotypes of two animals are identical or indistinguishable, this means only insofar as can be resolved with the methods used in this study.

SPECIMENS EXAMINED

All specimens from which chromosomes were examined are individually catalogued in the herpetological collections of the American Museum of Natural History (AMNH), the Museum of Natural History of Los Angeles County (LACM), the University of Arizona (UAZ), or the private collections of Mr. Ernest A. Liner (EAL) or Dr. Ralph W. Axtell (RWA). Catalogue numbers are in parentheses.

Sceloporus variabilis: COSTA RICA: *Guanacaste Prov.*: El Coco, sea level (AMNH 107701-107703, 107705, 107707, 107708). MEXICO: *Oaxaca*: Portillo Nejapa, 8 mi. SE El Camaron, 13 mi. (by Mex. Hwy. 190) SE Nejapa jct. (UAZ 29953). *Tamaulipas*: 83 mi. S Victoria, by road to Tampico (AMNH 113469). *Veracruz*: 23.8 mi. S Nautla (AMNH 113468); Ojo del Agua, Nacimiento del Rio Atoyac, ca. 10 km. (airline) NNE Córdoba (UAZ 18124). UNITED STATES: *Texas*: Uvalde Co.: 3 mi. (by Texas Hwy. 55) S Montell (UAZ 28246).

Sceloporus teapensis: GUATEMALA: El Ramate, Laguna Peten Itzá (UAZ 27701, 27702). *Alta Verapaz*: west end and west outskirts of Coban, *ca.* 1300 m. elev. (AMNH 115648). MEXICO: *Tabasco*: Playa Paraiso

(AMNH 114838, 114840). *Veracruz*: 2 mi. (by road) SE Sontecomapan, 14 mi. (by road) NE Catemaco (UAZ 29939, 29948, 29960).

Sceloporus cozumelae: MEXICO: *Yucatan*: 1.8 km. S Sisal (UAZ 18129, 19062, 19069). *Quintana Roo*: vicinity of the airport and to *ca.* 3 km. S thereof, Isla Mujeres (UAZ 19059); Ruin of Tulum (AMNH 110044).

Sceloporus parvus: MEXICO: *Nuevo Leon*: 10 mi. (by N. L. Hwy. 60) E San Roberto (AMNH 106511-106514).

Sceloporus couchii: MEXICO: Coahuila: 13 mi. E Cuatro Cienegas (39 mi. W Monclova) (UAZ 24243). *Nuevo Leon*: 3 mi. W Bustamante in Cañon Bustamante, Sierra de Gomas, 1300 ft. elev. (AMNH 115644, 115645); 6 mi. (by road) W Sabinas Hidalgo (AMNH 106390).

Sceloporus chrysostictus: MEXICO: *Yucatan*: Kabal Ruin (off Mex. Hwy. 261 S of Uxmal Ruin) (AMNH 110038).

Sceloporus jalapae: MEXICO: *Oaxaca*: 2 mi. (by road) E Mitla (UAZ 29922); 8 mi. SE El Tule, 13 mi. (by Mex. Hwy. 190) SE Oaxaca (UAZ 29920). *Puebla*: 1.5 mi. W Cacaloapan, 5500-5800 ft. elev. (AMNH 104457); 10 km. (by Mex. Hwy. 150 D [toll]) W Esperanza (AMNH 106440; UAZ 29919, 29934).

Sceloporus ochoterenae: MEXICO: *Guerrero*: 3.8 mi. (by Mex. Hwy. 95) N Chilpancingo (AMNH 106499, 106500, 106503).

Sceloporus siniferus: MEXICO: *Oaxaca*: 1 mi. S Animas Trujano, 5 mi. (by Mex. Hwy. 175) S Oaxaca (UAZ 29941); Juchitan (UAZ 29916); Puente Las Tejas, base of Cerro Quiengola, 7 mi. (by Mex. Hwy. 190) NW Tehuantepec (UAZ 29915, 29923, 29926, 29942, 29947).

Sceloporus scalaris: MEXICO: *Chihuahua*: 1.0 mi. NE (by road) Colonia Garcia (LACM 75310). *Michoacan*: 1 mi. W Villamar, 23 mi. (by Mex. Hwy. 15) W. Jacona (UAZ 29924, 29957). UNITED STATES: *Arizona*: Cochise Co.: *ca.* 0.2 mi. (by Barfoot Lookout Trail) W. Barfoot Rd., *ca.* 8950 ft. elev., Buena Vista Peak, Chiricahua Mts. (UAZ 19827, 19828, 20648); 0.5 mi. (by road to Long Park) S Rustler's Park, 8850 ft. elev., Chiricahua Mts. (UAZ 19826, 19829, 20644); trail to Barfoot Fire Lookout Tower, *ca.* 8400 ft. elev., Chiricahua Mts. (UAZ 29724). Santa Cruz Co.: *ca.* 0.5 mi. (by trail) below Bellows Spring, *ca.* 7500 ft. elev., Mt. Wrightston, Santa Rita Mts. (UAZ 19053).

Sceloporus aeneus: MEXICO: *Veracruz*: 9.3 mi. (by Mex. Hwy. 140) NE Perote (AMNH 106372, 106374-106376).

Sceloporus goldmani: MEXICO: *Coahuila*: 4.5 mi. SW Guadalupe Victoria, 6300 ft. elev. (AMNH 115642; EAL 4324-2, 4327); 3.5 km. N El Palmar (jct. Mex. Hwy. 54 and Gomez Farias road), 1955 m. elev., lat. 24°58′N long. 101°05′10″W (RWA 5670, 5671).

RESULTS AND DISCUSSION

The *variabilis* Group

Five species comprise the *variabilis* group as recognized by Smith (1939): *Sceloporus variabilis* Wiegmann, 1834; *S. teapensis* Günther, 1890; *S. cozumelae* Jones, 1927; *S. parvus* Smith, 1934; and *S. couchii* Baird, "1858" [1859?]. I describe the karyotype of *S. variabilis* in detail below and compare karyotypes of the other species with it.

Sceloporus variabilis: Examination of 42 cells from 11 individuals (seven males, four females) reveals a diploid number of 34 chromosomes ($2n=34$), which can be arranged in pairs and numbered in order of decreasing length (fig. 1A, B). There are six pairs of macrochromosomes and 11 pairs of microchromosomes. Of the macrochromosomes, numbers 1, 3, 4, and 5 are metacentric or nearly so, and numbers 2 and 6 are submetacentric. Generally the microchromosomes are too small to be resolved clearly, but as many as 10 of them have been seen to be bi-armed in some cells. One of the largest pairs of microchromosomes is distinctive, being subtelocentric and bearing a secondary constriction that appears as a gap near the centromere. No other consistent secondary constructions were observed in this species, which appears to lack the terminal satellites found on the long arm of chromosome number 2 in many other species of *Sceloporus*. In males, one microchromosome is minute, being smaller than all the others, whereas this is not so in females. Probably this minute is the Y chromosome, and *S. variabilis* has an XY(♂):XX(♀) sex chromosome system similar to that described in lizards of the genus

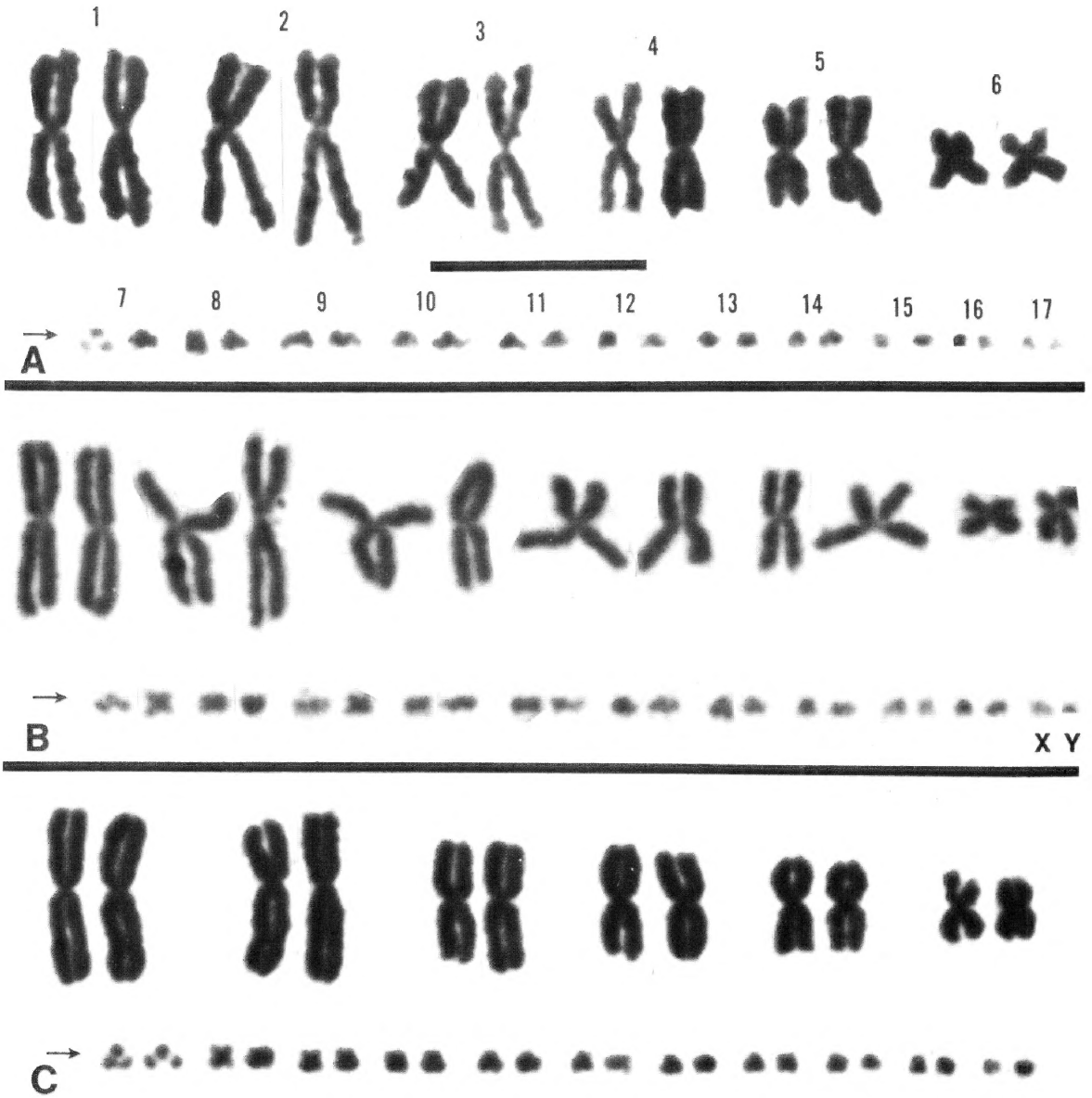

FIG. 1. Karyotypes of two species in the *variabilis* group of *Sceloporus*. A. *S. variabilis* ($2n=34$), ♀, AMNH 107703; line represents 10 μ. B. *S. variabilis* ($2n=34$), ♂, AMNH 113469; the minute Y is designated and paired with apparently the second smallest microchromosome in the cell, but whether this is the X is unknown. C. *S. teapensis* ($2n=34$), ♀, UAZ 29960. Arrows indicate positions of inconspicuous but characteristic secondary constrictions.

Uta by Pennock, Tinkle, and Shaw (1969) and similar to that found in some other species of *Sceloporus* (Cole, 1971a, b; also see descriptions below; fig. 2C).

The specimens examined include animals from opposite extremes (Texas and Costa Rica) of the geographic range of this polytypic species, including all the subspecies named: *S. v.*

variabilis Wiegmann, 1834; *S. v. marmoratus* Hallowell, 1852; *S. v. olloporus* Smith, 1937; and *S. v. smithi* Hartweg and Oliver, 1937.

Sceloporus teapensis: Examination of 37 cells from eight individuals (four males, four females) reveals a karyotype (fig. 1C) indistinguishable from that of *S. variabilis*. This includes the diploid number of chromosomes ($2n=34$), relative sizes and shapes, secondary constrictions on a pair of microchromosomes, and a minute Y.

Sceloporus cozumelae: Examination of 36 cells from five individuals (all males) reveals a karyotype (fig. 2A) that is similar or identical to that of *S. variabilis*. This includes the diploid number of chromosomes ($2n=34$), relative sizes and shapes, and secondary constrictions on a pair of microchromosomes. In some cells of these males it appears as though there is a minute Y microchromosome, but this is not so clear as in *S. variabilis*, and females of *S. cozumelae* are yet to be examined.

Sceloporus parvus: Examination of 17 cells from four individuals (two males, two females) reveals a karyotype (fig. 2B) similar or identical to that of *S. variabilis*. This includes the diploid number of chromosomes ($2n=34$), relative sizes and shapes, and secondary constrictions on a pair of microchromosomes (although they are not visible in the cell illustrated). In some cells of the males it appears as though there is a minute Y microchromosome, but this is not so clear as in *S. variabilis*. The specimens examined represent the subspecies *S. p. parvus* Smith, 1934.

Sceloporus couchii: Examination of 45 cells from four individuals (three males, one female) reveals a karyotype (fig. 2C) similar to that of *S. variabilis*, but with one conspicuous difference in centromere position; in *S. couchii*, chromosome number 5 is submetacentric rather than metacentric. Otherwise, similarities to the karyotype of *S. variabilis* include the diploid number of chromosomes ($2n=34$), relative sizes and shapes, secondary constrictions on a pair of microchromosomes, and a minute Y.

Summary of the *variabilis* Group

All species in the *variabilis* group as recognized by Smith (1939) have similar karyotypes, sharing the following combination of characteristics: a diploid number of 34 chromosomes with six pairs of metacentric or submetacentric macrochromosomes and 11 pairs of microchromosomes; secondary constrictions and satellites not conspicuous and probably lacking on chromosome number 2; one of the largest pairs of microchromosomes bearing a secondary constriction that appears as a gap near the centromere; an XY(♂):XX(♀) sex chromosome system, in which the sex chromosomes are microchromosomes and the Y is minute (yet to be confirmed in *S. cozumelae* and *S. parvus*). Of the numerous other species of *Sceloporus* that have been karyotyped, including representatives of most species and most species groups, only *S. chrysostictus* has the same combination of characteristics (Lowe, Wright, and Cole, 1966; Cole, Lowe, and Wright, 1967; Cole, 1970, 1971a, 1971b, 1972, 1975, and unpublished data; Hall and Selander, 1973). Other species that are karyotypically similar (e.g., *S. jalapae*, *S. siniferus*; see below) have a terminal satellite on the long arm of chromosome number 2, as do most species of *Sceloporus*, and lack a consistent secondary constriction on a large microchromosome. Therefore, I conclude that: (1) the microchromosome with a secondary constriction is derived; (2) the species within the *variabilis* group share this derived characteristic along with other traits that characterize the group (Smith, 1939, p. 236); (3) the *variabilis* species group is, therefore, a natural unit of closely related species and should be recognized as such (although the specific status of some populations needs further investigation; see below); (4) the status of the monotypic *chrysostictus* group as distinct from the *variabilis* group should be reconsidered (see below); and (5) consideration should be given to returning *Lysoptychus* to the synonymy of *Sceloporus* (see below).

Earlier (Cole, 1971a) I concluded that *S. chrysostictus* was more closely related to the *variabilis* group than to the *siniferus* group, where Smith (1939) thought its closest relationships existed. The karyotype of *S. chrysostictus* (see Cole, 1971a) is identical with that of *S. variabilis*, including the traits that characterize the *variabilis* group. My earlier studies of the karyotype of *S. chrysostictus* were based on four specimens (three males, one female).

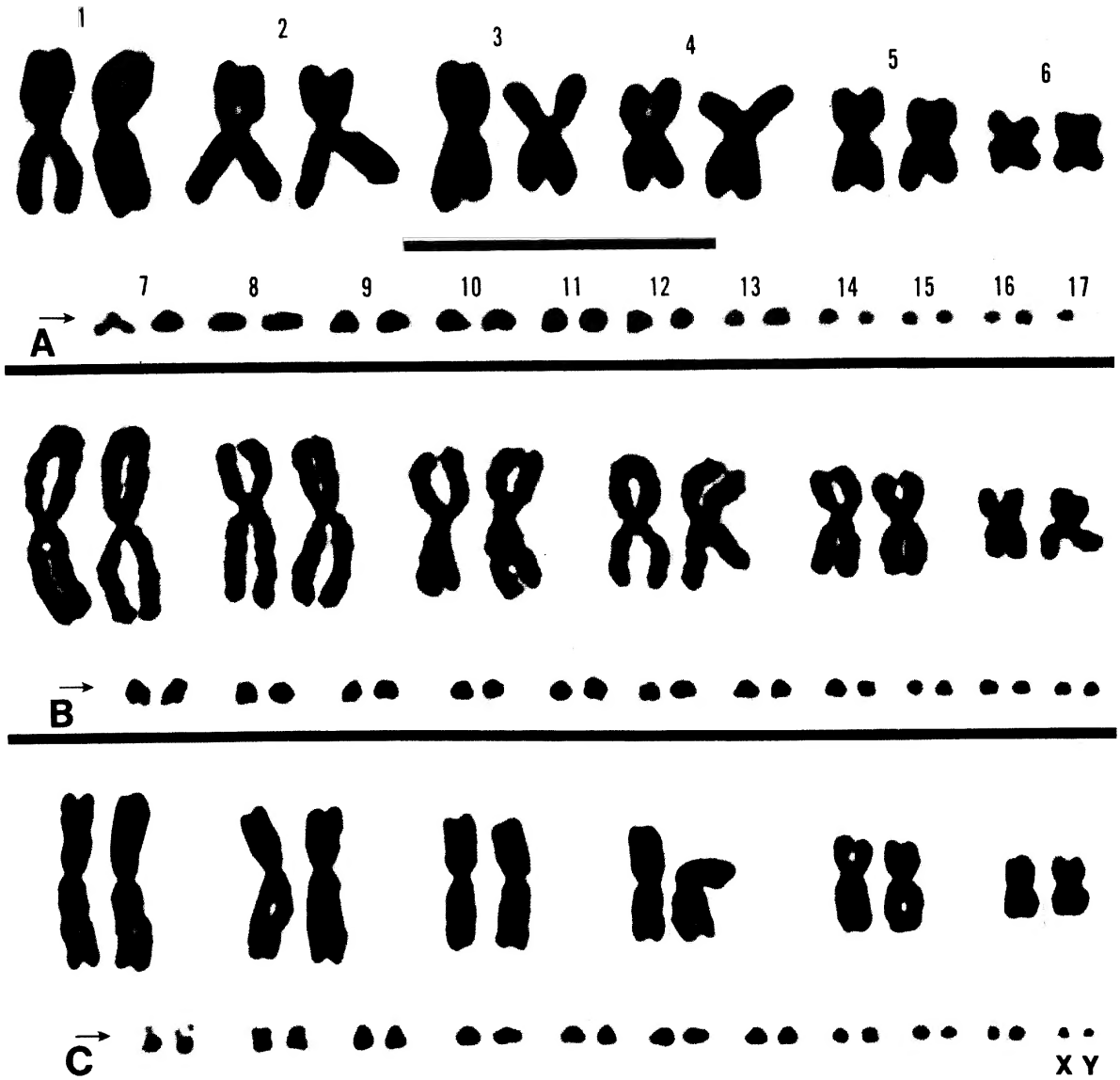

FIG. 2. Karyotypes of three species in the *variabilis* group of *Sceloporus*. A. *S. cozumelae* ($2n=34$), ♂, UAZ 18129; line represents 10 μ. B. *S. parvus* ($2n=34$), ♀, AMNH 106513. C. *S. couchii* ($2n=34$), ♂, UAZ 24243; the minute Y is designated and paired as in figure 1B. Arrows indicate positions of inconspicuous but characteristic secondary constrictions.

More recently I have examined chromosomes of six cells at mitotic metaphase from an additional female (see Specimens Examined), which had the same karyotype described. The similar and yet significantly different karyotype of *Sceloporus siniferus* is described below (fig. 3C).

Characteristics of external morphology also are consistent with the conclusion that the closest relatives of *S. chrysostictus* are in the *vari-*

abilis group. The following five traits that Smith (1939, p. 301) recognized, among others, as characterizing the *siniferus* group do not occur in *S. chrysostictus*: preanal scales keeled in females; postanals tending to be poorly developed in males; two postrostrals; lateral scales well-differentiated from dorsal scales; and ventral scales not notched. In contrast, only two of the traits that Smith (1939, p. 236) recognized as characterizing the *variabilis* group (postfemoral dermal pocket present; scales on posterior surface of thigh granular) do not occur in *S. chrysostictus*, and all or nearly all the traits that Smith (1939, p. 294) recognized as characterizing the *chrysostictus* group occur also in the species of the *variabilis* group. *Sceloporus cozumelae* is particularly similar to *S. chrysostictus*. Thus, there are only two characteristics (postfemoral dermal pocket; granular scales posteriorly on thigh) that distinguish the *variabilis* and *chrysostictus* species groups, whereas the karyotypic traits they share are unique in comparison with all other members of the genus karyotyped to date. I suggest that instead of stressing the differences by retaining the monotypic *chrysostictus* species group, *S. chrysostictus* should be considered hereafter as a member of the *variabilis* species group, reflecting the presumed common ancestry of the derived karyotypic traits they share. This is consistent with the conclusion of Larsen and Tanner (1975, p. 6), who placed *S. chrysostictus* in the *variabilis* group as they envisioned it (with the removal of *S. parvus* and *S. couchii*).

Larsen and Tanner (1975) resurrected the genus *Lysoptychus* Cope, 1888 for seven species that Smith (1939) had included in six species groups of *Sceloporus*. The seven species include *S. parvus* and *S. couchii* of Smith's *variabilis* group. The other five species included in *Lysoptychus* are: *gadoviae*, *merriami*, *maculosus*, *jalapae*, and *ochoterenae*, which Smith (1939) had placed in five different species groups (two monotypic and three having additional members that Larsen and Tanner retained in *Sceloporus)*.

Lysoptychus was characterized as follows: "(1) a postfemoral dermal pocket and less than 7 ventrals between the femoral pore series or (2) (if the postfemoral dermal pocket is absent) a vestigial gular fold and no postrostrals" (Larsen and Tanner, 1975, p. 18). These are not satisfactory as generic characteristics for the species included in *Lysoptychus* by Larsen and Tanner (1975) for the following reasons: (1) *couchii*, which has a postfemoral dermal pocket, also has more than seven ventrals between the femoral pore series, as have other species not included in *Lysoptychus* but included in Smith's *variabilis* group; (2) *jalapae* and *ochoterenae* have neither a postfemoral dermal pocket nor a vestigial gular fold; (3) thus, the combination of characteristics for recognizing *Lysoptychus* is not functional as presented; and (4) in some cases where the combination of characteristics does work I am not convinced that sharing these particular traits is a consequence of closest common ancestry. In addition, the chromosomal data, for reasons mentioned above, strongly indicate that the nearest evolutionary relationships of *parvus* and *couchii* are with species that Larsen and Tanner did not include within *Lysoptychus*, rather than with species included in *Lysoptychus* with them. I conclude that there is as yet no firm basis for recognizing the genus *Lysoptychus* Cope, 1888, and, therefore, I return it to the synonymy of *Sceloporus* Wiegmann, 1828.

It would not be reasonable to discuss the *variabilis* group as a whole without considering the specific status of its constituent species. Among them, the only taxon that I suspect does not warrant recognition as a biological species is *S. teapensis*. There is a strong superficial resemblance between the nominal *S. teapensis* and certain populations of *S. variabilis*, and, excepting a couple of questionable records in Guatemala (Smith, 1939, pp. 262, 283), they are parapatric in geographic distribution. I began to question the status of *teapensis* while identifying specimens collected personally as well as others received as gifts. Subsequent perusal of the literature showed that other investigators (e.g., Werler and Smith, 1952, p. 557) have questioned this also, although Smith (1937, 1939) had not directly compared *teapensis* with *variabilis* in his earlier reports. Indeed, Darling and Smith (1954, p. 189) stated, "Evidence that *S. teapensis* is specifically distinct

from *S. variabilis* has never been presented. There is no overlap in dorsal scale count of the former (36-47) and of *S. v. variabilis* (48-68), but there is of the former and *S. v. olloporus* (46-59), with which intergradation in Guatemala is quite possible. The remarkable similarity of *S. teapensis* and *S. variabilis* suggests conspecificity, especially in view of their closely juxtaposed ranges. Despite close approximation of range in southern Veracruz, it seems less likely that intergradation might occur there than in eastern Guatemala. At the present time no intergrades are known from anywhere, and despite overlap of characters of *S. teapensis* and all races of *S. variabilis* put together, it seems unwise to exchange one uncertainty for another by regarding the former as a race of the latter."

I pursued the question briefly by comparing the diagnostic, key, and descriptive characteristics of *S. teapensis* with those of *S. variabilis*, as presented by Smith (1939). In the process, I examined the characteristics on specimens of both species at the American Museum of Natural History, including series from various localities. The best characteristic for recognizing *teapensis* appeared to be the number of dorsal scales (occiput to rump), which was 36-47 (46-69 in *variabilis* but almost always more than 47). Although rare specimens of *variabilis* have fewer than 47 dorsals, no specimen of *teapensis* was known to have more than 47. Finally, I examined a series of four specimens (AMNH 114837-40) collected recently by Ms. Grace M. Tilger at Playa Paraiso, Tabasco, Mexico, which is well within the geographic range of *S. teapensis*, and found that number of dorsal scales ranged from 49 to 51, with a mean of 49.2.

Apparently there is more variation within *teapensis* than had been realized, and there is no firm basis for recognizing it as specifically distinct from *S. variabilis*. Indeed, the differences between *teapensis* and other populations of *S. variabilis* are of no greater magnitude than those that distinguish certain other populations of the polytypic *S. variabilis* from each other. Therefore, I conclude that the populations referred to as *S. teapensis* Günther, 1890 should be considered as a subspecies of *S. variabilis* Wiegmann, 1834 (*Sceloporus variabilis teapensis*, new combination), although I realize that the question of whether *teapensis* is a recognizable biological species will not be fully resolved until somebody completes a thorough analysis of geographic variation, including *Sceloporus variabilis* and samples from the areas where their ranges meet. *Sceloporus v. teapensis* is best distinguished from the other subspecies of *Sceloporus variabilis* by its relatively low number of dorsal scales (36-51).

In summary, I conclude that the *variabilis* species group consists of the following five species of *Sceloporus*: *S. variabilis*, *S. chrysostictus*, *S. couchii*, *S. cozumelae*, and *S. parvus*.

The *jalapae* Group

Two species comprise the *jalapae* group as recognized by Thomas and Dixon (1976): *Sceloporus jalapae* Günther, 1890; and *S. ochoterenae* Smith, 1934. I describe the karyotype of *S. jalapae* in detail below and compare that of *S. ochoterenae* with it. I also describe the karyotype of *Sceloporus siniferus* Cope, 1869, of Smith's (1939) *siniferus* species group, as Smith had considered *S. ochoterenae* as a member of the *siniferus* group. Karyotypes of the species in the *scalaris* species group, to which Smith (1939) had assigned *S. jalapae*, are presented later in this paper.

Sceloporus jalapae: Examination of 43 cells from six individuals (five males, one female) reveals a diploid number of 34 chromosomes ($2n=34$), which can be arranged in pairs and numbered in order of decreasing length (fig. 3A). There are six pairs of macrochromosomes and 11 pairs of microchromosomes. Of the macrochromosomes, numbers 1, 3, 4, and 5 are metacentric or nearly so, and numbers 2 and 6 are submetacentric. There is a small terminal satellite on the long arm of chromosome number 2. Generally the microchromosomes are too small to be resolved clearly, but as many as six of them have been seen to be bi-armed in some cells. In some cells of the males it appears as though there is a minute Y microchromosome, but this is not so clear as in *S. variabilis*, so I cannot as yet conclude that there is a minute Y in *S. jalapae*.

Sceloporus ochoterenae: Examination of 10

cells from three individuals (one male, two females) reveals a karyotype (fig. 3B) similar or identical with that of *S. jalapae*. This includes the diploid number of chromosomes ($2n=34$), relative sizes and shapes, and the terminal satellite on the long arm of chromosome number 2. As in *jalapae*, the question of whether there is a minute Y chromosome in males remains open.

KARYOTYPE OF *Sceloporus siniferus*

Examination of 28 cells from seven individuals (three males, four females) reveals a

FIG. 3. Karyotypes of species in the *jalapae* and *siniferus* groups of *Sceloporus*. A. *S. jalapae* ($2n=34$), ♂, UAZ 29920; line represents 10 μ. B. *S. ochoterenae* ($2n=34$), ♂, AMNH 106499. C. *S. siniferus* ($2n=34$), ♀, UAZ 29942. Arrows indicate positions of inconspicuous but characteristic secondary constrictions and satellites.

karyotype (fig. 3C) similar or identical to that of *S. jalapae*. This includes the diploid number of chromosomes ($2n=34$), relative sizes and shapes, and the terminal satellite on the long arm of chromosome number 2. As in *jalapae*, the question of whether there is a minute Y chromosome in males remains open. The specimens examined all represent the subspecies *S. s. siniferus* (see Smith and Taylor, 1950, p. 134, for a discussion of the subspecies).

Summary of the *jalapae* Group

Larsen and Tanner (1975) included *jalapae* and *ochoterenae* in the genus *Lysoptychus* (which I have returned to the synonymy of *Sceloporus*, above), emphasizing their conclusions that *jalapae* does not belong in the *scalaris* species group (Smith, 1939) and that *ochoterenae* does not belong in the *siniferus* species group (Smith, 1939). Thomas and Dixon (1976) also thought that Smith's (1939) placement of *jalapae* and *ochoterenae* did not best reflect their relationships, and particularly their close relationship to each other, so they placed them together "in a group of their own, the *jalapae* group" (Thomas and Dixon, 1976, p. 525). Having reviewed the evidence and the discussions, particularly as presented by Thomas and Dixon (1976), I concur with the provisional recognition of the *jalapae* species group (although it has not as yet been clearly defined), which emphasizes the close relationship of these two species. The fact that *S. jalapae* and *S. ochoterenae* have very similar or identical karyotypes is consistent with this decision.

The species of the *scalaris* species group have karyotypes (see below, fig. 4) that are rather different from that characterizing the *jalapae* group, which also is consistent with the removal of *S. jalapae* from the *scalaris* group. *Sceloporus siniferus* is the only species I have karyotyped as yet from the *siniferus* group, in which Smith (1939) had included *S. ochoterenae*. Its karyotype (fig. 3C) is similar or identical with that of the species in the *jalapae* group and with that of some other species representing several species groups of *Sceloporus* (e.g., *S. utiformis* Cope, 1864; Cole, 1971a, pp. 13-14).

The *scalaris* Group

Three species comprise the *scalaris* group as recognized by Thomas and Dixon (1976): *Sceloporus scalaris* Wiegmann, 1828; *S. aeneus* Wiegmann, 1828; and *S. goldmani* Smith, 1937. I describe the karyotype of *S. scalaris* in detail below and compare karyotypes of the other species with it.

Sceloporus scalaris: Examination of 57 cells from 11 individuals (seven males, four females) reveals a diploid number of 24 chromosomes ($2n=24$), which can be arranged in pairs and numbered in order of decreasing length (fig. 4A). There are six pairs of macrochromosomes and six pairs of distinctly smaller chromosomes. Of the macrochromosomes, numbers 3 and 4 are metacentric and numbers 1, 2, 5, and 6 are submetacentric. There is a small terminal satellite on the long arm of chromosome number 2. I do not refer to the smaller chromosomes as microchromosomes because many or most of them (probably at least the four largest pairs) are approximately twice the size of the microchromosomes observed in other species of *Sceloporus* (see discussion in Cole, 1971a, p. 6, concerning *S. graciosus* Baird and Girard, 1852). Although the shapes of the smaller chromosomes are difficult to resolve in many cells, on a few occasions as many as 10 of the 12 have been seen clearly to be bi-armed within a single cell, with most of the largest ones appearing metacentric or submetacentric. No sex-correlated heteromorphic pairs of chromosomes were observed.

Sceloporus aeneus: Examination of 19 cells from four individuals (one male, three females) reveals a karyotype (fig. 4B) similar to that of *S. scalaris*. This includes the diploid number of chromosomes ($2n=24$), relative sizes and shapes of most pairs, and the terminal satellite on the long arm of chromosome number 2. The macrochromosomes appear to be the same as those of *S. scalaris* except for chromosome number 1, which is metacentric to submetacentric in most cells from *aeneus*, whereas it is clearly submetacentric in *scalaris*. The smaller chromosomes appear highly similar to those of *S. scalaris* also, although only as many as six have been seen clearly to be bi-armed within a single cell, and the second largest pair (no. 8)

in *aeneus* may have a more terminal centromere than it has in *scalaris*.

Sceloporus goldmani: Examination of 25 cells from five individuals (one male, four females) reveals a karyotype (fig. 4C) identical with that of *S. scalaris*. This includes the diploid number of chromosomes ($2n=24$), relative sizes and shapes, and the terminal satellite on the long arm of chromosome number 2. In a few cells, all 12 of the smaller chromosomes have been seen clearly to be bi-armed.

Summary of the *scalaris* Group

All the species in the *scalaris* group as recognized by Thomas and Dixon (1976) have

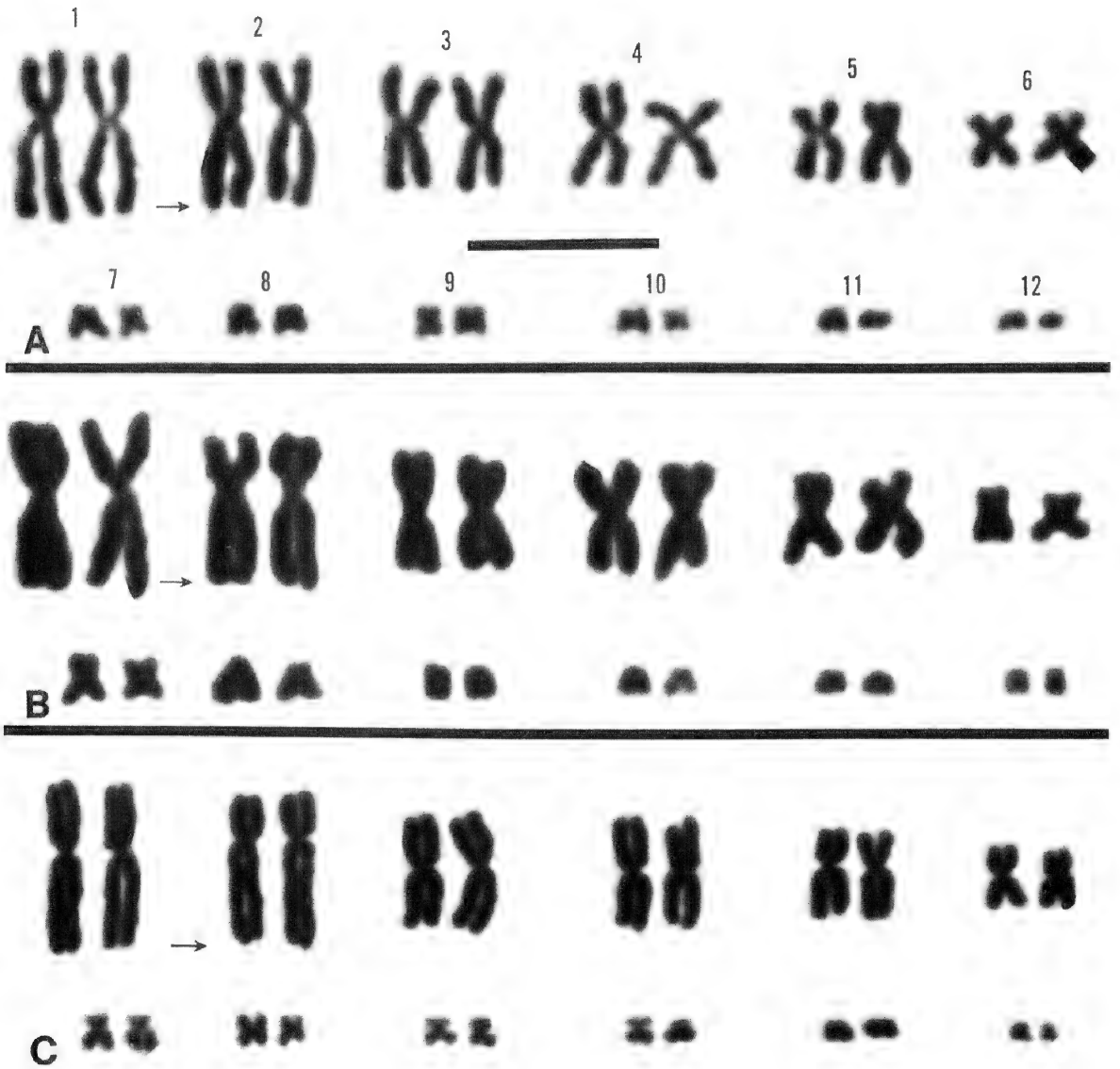

FIG. 4. Karyotypes of the three species in the *scalaris* group of *Sceloporus*. A. *S. scalaris* ($2n=24$), ♂, UAZ 19826; line represents 10 μ. B. *S. aeneus* ($2n=24$), ♂, AMNH 106376. C. *S. goldmani* ($2n=24$), ♀, RWA 5671. Arrows indicate positions of inconspicuous but characteristic secondary constrictions and satellites.

highly similar karyotypes. Moreover, a certain combination of karyotypic characteristics is shared by these species and only these species among all members of the genus that have been karyotyped to date, which includes by far the majority of the species in the genus. This combination of characteristics is: a diploid number of 24 chromosomes with six pairs of macrochromosomes and six pairs of smaller chromosomes, many or most of which are too large to be referred to as microchromosomes; a terminal satellite on the long arm of chromosome number 2; and chromosome number 5 being submetacentric. Since these characteristics are shared only by these species among all those karyotyped in the genus, the karyotypic data are consistent with the recognition of the *scalaris* group as reviewed by Thomas and Dixon (1976). This also is consistent with the decisions (Larsen and Tanner, 1975; Thomas and Dixon, 1976) to remove *S. jalapae* from the *scalaris* group as recognized by Smith (1939), which I discussed above.

CONCLUSIONS

1. The genus *Lysoptychus* Cope, 1888 is returned to the synonymy of *Sceloporus* Wiegmann, 1828. All seven species assigned to *Lysoptychus* by Larsen and Tanner (1975) are valid species of *Sceloporus*.

2. The monotypic *chrysostictus* species group should not be recognized; *S. chrysostictus* belongs in the *variabilis* species group.

3. The species of the *variabilis* group karyotypically are similar to each other and distinctly different from all other species in the genus that have been karyotyped to date, which is consistent with recognition of the *variabilis* species group.

4. The populations previously referred to as *Sceloporus teapensis* are best recognized as a subspecies of *Sceloporus variabilis* (*Sceloporus variabilis teapensis*, new combination).

5. Five species comprise the *variabilis* species group: *S. variabilis*, *S. chrysostictus*, *S. couchii*, *S. cozumelae*, and *S. parvus*.

6. The two species comprising the *jalapae* species group (*S. jalapae*, *S. ochoterenae*) have very similar or identical karyotypes, which is consistent with recognition of the group. The karyotypes are very different from those of the *scalaris* species group, with which *S. jalapae* has been grouped in the past, but they are very similar or identical with that of *S. siniferus*, with which *S. ochoterenae* had been grouped by Smith (1939).

7. The three species of the *scalaris* group (*S. scalaris*, *S. aeneus*, *S. goldmani*) karyotypically are similar to each other and distinctly different from all other species in the genus that have been karyotyped to date, which is consistent with recognition of the *scalaris* species group.

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